NEST SUCCESS AND AGE-SPECIFIC MORTALITY IN TRAILL'S FLYCATCHERS

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THIS paper presents nest success, factors affecting nest success, agespecific mortality from egg-laying until fledging, and a crude estimate of the mean number of fledglings produced per pair in Traill's Flycatchers (*Empidonax t. traillii*). I studied a total of 106 nests in five summers from 1963–1967 at Toledo, Ohio, 1963–65; Fremont, Nebraska, 1966; and Wooster, Ohio, 1967. I visited nests at least once daily and tried to find them before construction or egg-laying was completed.

The habitat in Toledo was old fields and ditch banks, and was the same area in which I studied American Goldfinches (*Spinus tristis*) (Holcomb, 1969a). I measured nest heights to the nearest 0.5 inch from the ground to the top rim of the nest. Unhatched eggs were opened within 2 days after the other nestlings hatched to determine at what stage embryonic development ended.

RESULTS AND DISCUSSION

Nest success.—I found 91 nests in which the number of eggs laid and numbers of young fledged could be determined exactly. The 91 nests had 272 eggs from which 99 young fledged for a total success of 36.4 percent. Of 272 eggs, 149 or 54.8 percent hatched. Factors involved in reduction of nest success were: 6 infertile eggs, 3 embryos interrupted in development, 96 eggs removed by predators, 41 nestlings removed by predators, 8 eggs and 1 nestling destroyed by rain and windstorms, 7 nestlings that starved when abandoned by adults (at least one adult of two pairs probably died or was caught by a predator), 4 eggs not hatching because of Brown-headed Cowbird (*Molothrus ater*) egg, 3 eggs lost through weak nest construction, and 4 eggs abandoned because of human interference.

Of 91 nests that could have produced young, 36 nests or 39.5 percent fledged at least one young. The 89 nests in which I knew the exact numbers of eggs and fledglings produced 99 fledglings for a mean of 1.11 fledglings per nest.

Both Walkinshaw (1966) and Berger (1967) reported much higher nesting successes than this. Walkinshaw reported 65.2 percent of 92 nests produced at least 1 fledgling and 65.6 percent of 302 eggs produced fledglings with an average of 3.2 young produced per pair in 23 pairs. Berger reported 69.5 percent of 207 nests producing at least 1 fledgling and 89.5 percent of 362 eggs laid in 96 nests produced fledglings.

OF CONSTRUCTION											
	Nests below 52.5 inches	Nests 52.5 inches or above	First nests	Renests							
Nests	45	35	50	36							
Eggs laid	146	113	170	102							
Young fledged	62	37	63	36							
Percent eggs produced fledglings	42.5	32.7	37.1	35.3							

TABLE 1 SUCCESS OF TRAILL'S FLYCATCHER NESTS COMPARED WITH HEIGHT OF NEST AND TIME OF CONSTRUCTION

Nest success in relation to nest height and building date.—Number of eggs laid, number of young fledged, and height of nests were determined for 80 nests. The median height was 52.5 inches. Table 1 shows higher nests were less successful than lower nests.

All first nests of a season were started before 20 June and nearly all renests 20 June or later. Table 1 shows that nest success in first nests (37.1 percent) is not significantly different from that of renests (35.3 percent).

Holcomb and Twiest (1968) and Meanley and Webb (1963) reported better nest success for Red-winged Blackbirds (*Agelaius phoeniceus*) in higher than in lower nests. Holcomb (1969a) found that nest success in the American Goldfinches increased with nest height. Longcore and Jones (1969) reported nest success of the Wood Thrush (*Hylocichla mustelina*) to be inversely proportional to nest height, and nests were more successful as the season progressed.

Age-specific mortality.—Table 2 shows the times when eggs or nestlings were destroyed by the several factors listed above. Eggs were removed regularly by predators throughout egg-laying and the first two-thirds of the incubation period. Only five eggs were removed in the final third of the incubation period. The only explanation I can suggest is that adults may behave differently and attract less attention during this interval. Nestling predation was greatest in the first two-thirds of the nestling period. This is similar to Holcomb's (1969b) data for American Gold-

 TABLE 2

 TIMES OF MORTALITY OR DISAPPEARANCE OF EGGS AND NESTLINGS

	Day									ľ					
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Eggs during laying Eggs during incubation	27	9 12	7 3	1 6	1	15	10	7	4				4		1
Nestlings	2	5	15	2	6	2	1	8		8					



Figure 1. Survival of flycatcher eggs and nestlings. Days in nest refers to the time from egg laying, extending through incubation and nestling periods. The mean incubation period was 13.3 days.

finches, which fledged at a mean of 12.3 days with no predation after day 9. Loss of younger nestlings may be due to the greater activity of adults feeding nestlings, and the movements and sounds made by nestlings. The loss of two nests of abandoned young also occurred in this interval. Probably at least one adult from each of these nests was taken by a predator during this demanding period.

Figure 1 is a survival curve for the Traill's Flycatchers on a semilogarithmic scale in which a uniform rate of mortality results in a straight line. The rate of removal of eggs is fairly uniform in the egglaying period and during the first two-thirds of incubation, with a marked decrease in mortality in the last third of incubation. The rate of mortality in the nestling period was uniform throughout the first twothirds with no mortality in the last third. It is remarkable that no nestlings were removed after day 9, even though the mean age of 81 fledgings was 12.5 days with a range of 11–14 days and the mode at 12 days. This same pattern was present in goldfinches that nested in the same type of vegetation and habitat. I suggest as I did for the goldfinches that the older nestlings are more aware of their environment and remain quiet when potential predators approach. Also by the time nestlings are older, many have already been removed from more conspicuous nests or from nests where the adults behave more conspicuously. Rainstorms killed only one nestling on day 3. Nestlings are more vulnerable to cool, wet weather at younger ages.

From his survival curves for Red-winged Blackbirds and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) Young (1963) suggested that positively skewed life curves appear to be typical for small passerines, which is confirmed by the present data on Traill's Flycatchers and my (1969b) data for goldfinches.

Fledglings produced per pair.—In 1965–1967 I was able to identify the activities of 29 pairs of birds. Walkinshaw (1966) reported Traill's Flycatchers do not try to raise a second brood in a summer, but commonly renest after an unsuccessful attempt. The 29 pairs of birds in this study built 49 nests in which 41 young fledged for a mean of 1.69 nests per pair, 0.84 fledglings per nest and 1.41 young per pair. I suspect that 1.41 young per pair is a low value and may be due partly to my more intensive studies of these pairs. A value of 1.88 young fledged per pair is obtained if 1.11 young per nest is multiplied by a mean of 1.69 nests for each pair. This value remains far below the 3.2 value Walkinshaw (1966) reported.

Using Walkinshaw's (1966) data on returns of banded adult Traill's Flycatchers and his value of 3.2 young fledged per pair, 23 pairs fledged a total of 74 young. His approximate mortality of 30.1 percent of the adults of the population would necessitate a replacement of (30.1×46) adults) nearly 14 birds by the first-year group to maintain the population. This is only 19 percent of the young fledged the previous year. The highest mortality rates appear to be in the earliest stages as reported by Young (1963), Holcomb (1969b), and in this paper. However an 81 percent mortality from time of fledging to time of return for breeding does appear rather high. I suggest that the value of 3.2 young raised per pair reported by Walkinshaw is probably high. If the approximate value of 1.41 young per pair that I calculated is substituted for Walkinshaw's 3.2 young, mortality from time of fledging to time of returning to breed would be about 38 percent (assuming 1.41 young/pair \times 26 pairs = 37 young, with a need for 14 replacements). The value of 38 percent mortality from fledging to first breeding appears rather low. On the basis of these crude approximations I suggest that mean numbers of fledged young per pair in Traill's Flycatchers is between 2.0 and 3.0 per year.

Walkinshaw's 30.1 percent return was on birds banded as adults of unknown age; probably adult mortality between a first and second breeding season is nearer 50 percent according to the survival rates reported by Fankhauser (1967) on Red-winged Blackbirds and Farner's review (1945) for several passerine species.

SUMMARY

Factors involved in Traill's Flycatcher nest success were studied from 1963–1967. From a total of 272 eggs in 91 nests, 99 young fledged for a success of 36.4 percent. Predators accounted for most failures. Nest success was inversely proportional to nest height, but no difference was evident in success of first nests or renests.

Age-specific mortality evaluations depict a positively skewed mortality curve in the life of Traill's Flycatchers. A survival curve until fledging shows that most eggs are removed by predators in the first two-thirds of incubation and that no nestling predation occurred after day 9 even though mean age of fledging was 12.5 days.

A crude estimate made of the mean number of fledglings required per pair to compensate for adult mortality in the following year suggests that between 2.0 and 3.0 fledglings produced for each pair per year should maintain a population.

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